

VERTICAL DISTRIBUTION OF ADULT FISH IN PYRAMID LAKE, NEVADA¹

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ABSTRACT.— Inshore and limnetic vertical distribution of adult fish in Pyramid Lake, Nevada was determined from late spring to early fall 1977. The benthic (23 m) inshore area exhibited a relatively diverse composition of five species, while the inshore surface and offshore limnetic zones were composed of over 98 percent tui chubs (*Gila bicolor*). Vertical fish distribution was associated with temperature and zooplankton distribution.

Prior to the Pyramid Lake Ecological Study, 1975–1978, limited data were available on the relative abundance, distribution, and environmental relationships of Pyramid Lake fish populations. Historically, Snyder (1917) made observations on the life histories, seasonal movements, and spawning migrations of fishes occurring in the lake. Sumner (1938, 1939) documented the decline of the Lahontan cutthroat trout, *Salmo clarki henshawi*, and related factors responsible for the ultimate extinction of the pure Pyramid Lake strain. After successful reintroduction of salmonids into Pyramid Lake in the early 1950s the Nevada Fish and Game Department conducted life history investigations of the fish species during 1954–58, including limited population inventory (Johnson 1958). Koch (1972, 1973) studied the ecology and reproductive characteristics of the endangered, endemic cui-ui, *Chasmistes cujus*, with reference to environmental conditions that may become limiting to this species. During recent years, the United States Fish and Wildlife Service has been monitoring cui-ui population trends in the vicinity of the Truckee River delta and spawning runs of Lahontan cutthroat trout through the Marble Bluff fish passage facility.

Conflicts over water resource utilization of the Truckee River-Pyramid Lake ecosystem have indicated a need for a reliable as-

essment of its fishery resource. Distribution and abundance data on the fish populations of Pyramid Lake in relation to environmental conditions are essential to such an assessment. With adequate data on the ecosystem dynamics of Pyramid Lake, an understanding of the effects of potential changes in environmental conditions on the lake's fish populations may be achieved.

The purpose of this research was to describe the vertical distribution of fish in Pyramid Lake. Secondly, relationships between spatial fish distribution, and temperature and zooplankton distribution are presented.

STUDY AREA

Pyramid Lake is the deepest remnant of Pleistocene Lake Lahontan, which once occupied an area of 5,006,490 ha from west-central Nevada, north to the Oregon border (Russell 1885). Pyramid Lake is approximately 40 km long and 6.5 to 16 km wide. The upper two-thirds of the lake has an oval shape and a north-south axis, while the relatively narrow and shallow lower third is rectangular with a southeasterly axis. At the mean 1976 elevation of 1,157.3 m (United States Geological Survey 1977), the lake had a surface area of 44,637 ha, volume of $2.638 \times 10^{10} \text{m}^3$, mean depth of 59 m, and maximum depth of 103 m (Harris 1970).

¹The Pyramid Lake ecological study was conducted by W. F. Sigler & Associates, Inc., under contract (#H50C14209487) to the United States Department of Interior, Bureau of Indian Affairs.

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Being the terminal water body of the endorheic Truckee River system, the only outflow from Pyramid Lake is by evaporation. Due to water diversions from the Truckee River, the water level of Pyramid Lake has declined 22 m since 1909. At present the lake water is highly ionic, being saline, alkaline, and basic (pH = 9.2). The 1976 total dissolved solids (TDS) concentration of 5,235 mg/l was composed of 68 percent sodium chloride (Edward L. Linder, pers. comm.). The lake may be considered eutrophic because it supports large plankton and fish populations.

Water temperature seasonally ranges from 0.6 to 25.5 C (Koch 1973). As winds subside and surface water temperature increases, a thermocline develops during June and persists through December. Following physical destratification, the turnover begins in early winter and mixing extends to spring. Pyramid Lake is thus classified as monomictic (Hutchinson 1957).

PROCEDURES

Surface and bottom gill nets were fished along the 23 m depth contour on the east and west sides of the north, middle, and south sections of Pyramid Lake. Concurrently, gangs of vertical gill nets were fished in the center of Pyramid Lake, in the deepest area (90 m+). Thus, six inshore surface-bottom stations (stratified by lake area) and one limnetic water column station were sampled on a monthly basis (Fig. 1).

Surface-bottom gill nets were test-fished from February through May 1977 (12 samples), and intensively fished from June through November 1977. During this period, 35 surface samples above the thermocline and 35 bottom samples below the thermocline, at a depth of 23 m, were taken.

The bottom gill nets were 1.83 m deep and 76.20 m in length. The nets were composed of ten 1.83 × 7.62 m panels of the following mesh sizes (cm bar measure): 1.27, 1.91, 2.54, 3.18, 3.81, 4.45, 5.08, 6.35, 7.62, and 8.89. The 76.20 m surface gill nets were identical to the bottom-set nets except they were 3.66 m instead of 1.83 m deep

and rigged to float on the surface instead of sinking to the bottom.

Vertical gill nets (four mesh sizes) were test-fished in offshore areas from December 1975 through February 1976; however, bad weather made the sampling inefficient and the catch rate was very low, apparently due to the large mesh sizes used. I implemented an intensive vertical gill netting program from June through October 1977. A total of 18 sets of gangs of eight graduated mesh sizes were made at the midlake limnetic station during this period, on a monthly basis.

The vertical gill nets were similar to those described by Horak and Tanner (1964). The nets were anchored at a bottom depth of over 90 m, and extended from the surface to about 46 m. Spreader bars physically separated each net into six 7.62 m depth increments. The nets, 2.44 × 45.72 m, were set in gangs of eight nets of the following mesh sizes (cm bar measure): 1.27, 1.91, 2.54, 3.81, 5.08, 6.35, 7.62, and 8.89.

All nets were built of white multifilament nylon. The thread diameters (for respective mesh sizes) were 0.23 mm (1.27 cm), 0.28 mm (1.91 and 2.54 cm), 0.33 mm (3.18, 3.81, 4.45, 5.08, and 6.35 cm), and 0.40 mm (7.62 and 8.89 cm).

Distribution was evaluated with respect to catch/effort. The unit-of-effort was defined as a one-day (approximately 24 hours) gill net set.

RESULTS AND DISCUSSION

The benthic (23 m) inshore area exhibited a relatively diverse species composition: tui chub (*Gila bicolor*), Tahoe sucker (*Catostomus tahoensis*), Lahontan cutthroat trout, cui-ui, and Sacramento perch (*Archoplites interruptus*). In contrast, Tahoe suckers, cui-ui, and Sacramento perch were rare in the inshore surface waters and absent in the limnetic zone. Over 98 percent of the catch in the surface-inshore and limnetic zones were composed of tui chubs; the remainder was primarily Lahontan cutthroat trout.

Tahoe suckers were almost entirely benthic in habitat; 99.7 percent of the catch at 23 m was taken on the bottom (Table 1). McConnell et al. (1957) found the Utah

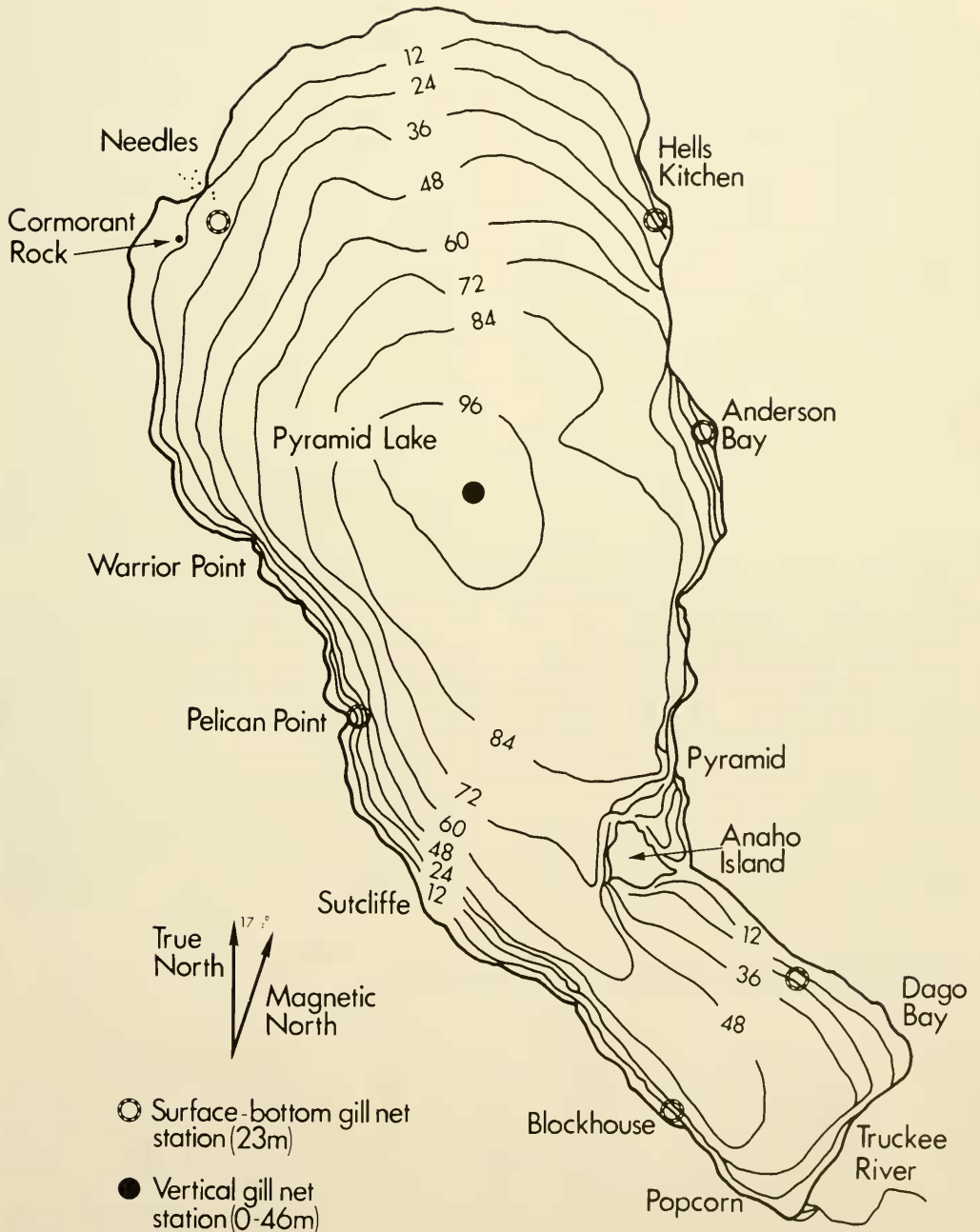


Fig. 1. Gill net sampling stations (six inshore and one limnetic) in Pyramid Lake, Nevada.

sucker, *Catostomus ardens*, exclusively on the bottom of Bear Lake, concentrated at depths of 7.5–23 m. This benthic behavioral preference is characteristic of the genus *Catostomus*. These suckers exhibit extreme specialization and orientation of the jaws, general morphological adaptations (inferior mouth, numerous papillae and taste buds, limited eyesight, and position of eyes in the head), and behavioral modifications for suctional feeding (Martin 1972); all of these adaptations are indicative of obligatory bottom dwellers.

The cui-ui is a lacustrine sucker (*Catostomidae*), endemic to Pyramid Lake. The diet of this species consists almost exclusively of zooplankton (Johnson 1958, LaRivers 1962); and it has therefore been hypothesized that cui-ui inhabit open limnetic waters where zooplankton are abundant (LaRivers 1962). My findings indicate, however, that cui-ui are inshore oriented—they were never captured in the midlake limnetic area. Cui-ui were concentrated in the littoral zone (0–15 m) and were never taken in benthic areas deeper than 46 m (Vigg 1978a). Cui-ui were infrequently captured at 23 m, either on the surface or bottom. The only surface catch occurred during spring corresponding to their spawning season; the maximum benthic catch of cui-ui at 23 m occurred during fall as surface water temperatures were decreasing. The catch rate of Sacramento Perch at 23 m was extremely low (mean of 0.06/net), however the seasonal pattern was similar to that of the cui-ui.

Cutthroat trout and tui chub exhibited temporal changes in vertical inshore distribution which were associated with surface

water temperature (Fig. 2). The maximum surface distribution of cutthroat trout occurred during April and May. When the surface water temperature increased from the May level of 10.3 to 16.3 C in June the cutthroat trout moved almost entirely out of the surface waters (less than 5 percent of the catches were taken in the surface nets). The lowest seasonal density of cutthroat trout occurred in surface waters (0.68/net), and the highest density occurred in benthic waters below the thermocline (8.42/net) during the summer period. As surface waters cooled from 16.5 C in October to 14.5 C in November, the proportion of cutthroat trout captured on the surface began to increase. Judging from the December temperature of about 11 C, the proportion of the cutthroat trout population inhabiting surface waters probably continued to increase during early winter. This distribution pattern indicates that the Lahontan cutthroat trout are predominantly benthic in their distribution throughout the year, but they prefer areas exhibiting the temperature range of 7–15 C in Pyramid Lake under natural conditions.

The cutthroat trout catch offshore in the limnetic zone was relatively low and exhibited substantial vertical dispersion (Table 2). About 69 percent of the total catch from June through October was taken at depths of 15 to 37.5 m, at temperature ranges of 11.2–18.5 C and 7.5–8.1 C, respectively. During the entire period, the 37.5–45.0 m depth stratum (at temperatures <7.5 C) exhibited the lowest trout catches. No trout were captured in the upper 7.5 m during

TABLE 1. Fish catch in the surface (3.66 × 76.2 m gill net) and bottom (1.82 × 76.2 m gill net) zones at the 23 m depth contour of Pyramid Lake, from June through November 1977.

Depth zone	Catch statistic	Species					Total
		Cutthroat trout	Cui-ui	Tahoe sucker	Tui chub	Sacramento perch	
Surface	Number	47	0	2	2,657	1	2,707
	Catch/net	1.34	0	0.06	75.91	0.03	77.34
	Percent by species	1.7	0	0.07	98.2	0.04	100
	Percent by depth	14.8	0	0.03	57.4	25.0	48.4
Bottom	Number	270	10	631	1,975	3	2,899
	Catch/net	7.71	0.29	18.03	56.43	0.09	82.54
	Percent by species	9.3	0.4	21.8	68.4	0.1	100
	Percent by depth	85.2	100	99.7	42.6	75.0	51.6

July and August, at temperatures ranging 20.6–23.2 C.

Temperature is generally considered the major directive influence on vertical fish distribution in lakes; dissolved oxygen is a secondary effect, restricting fish distribution where anaerobic conditions occur (Dendy 1948, Borges 1950, Ferguson 1958, Horak and Tanner 1964, von Geldern 1964, May 1973, Gebhart and Summerfelt 1975, and Lindenberg 1976). In Walker Lake, Nevada, high surface water temperatures interact with hypolimnetic oxygen deficits during summer to restrict cutthroat trout to a narrow zone in the vicinity of the thermocline (Cooper 1978). In Pyramid Lake, however, I found low dissolved oxygen concentrations to restrict fish distribution only in the profundal zone during late fall prior to lake mixing (Vigg 1978a).

Horak and Tanner (1964), and von Geldern (1964) found the majority of rainbow trout (*Salmo gairdneri*) distributed in depth intervals exhibiting the temperature range 15.5–21.0 C. Fast (1973) and Overholtz et al. (1977) also found rainbow trout dis-

TABLE 2. Catch of cutthroat trout and tui chub in depth strata of the limnetic zone of Pyramid Lake, from June through October 1977.

Depth interval (m)	Cutthroat trout		Tui chub	
	Number	Percent	Number	Percent
0–7.5	5	14.3	1,962	37.5
7.5–15	5	14.3	1,900	36.4
15–22.5	9	25.7	935	17.9
22.5–30	6	17.1	232	4.4
30–37.5	9	25.7	195	3.7
37.5–45	1	2.9	3	0.05
TOTAL	35	100	5,227	100

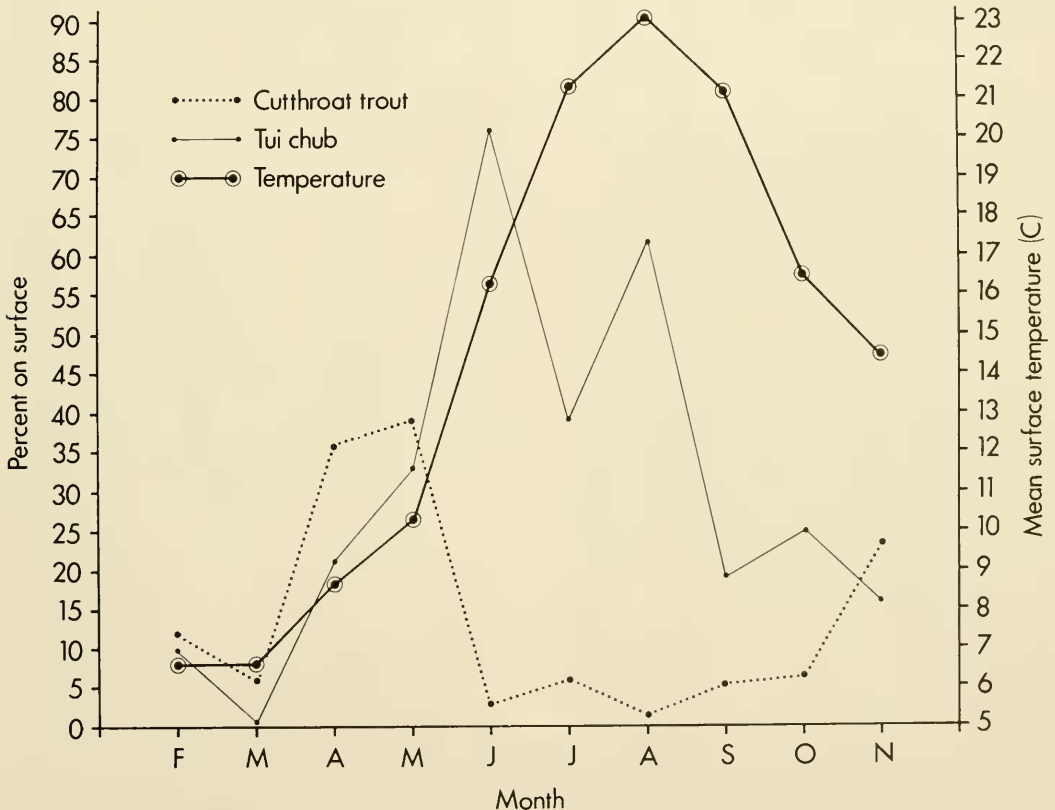


Fig. 2. Percent of the catches of cutthroat trout and tui chub taken on the surface; from surface and bottom gill nets (adjusted to unit of net area) at the 23 m depth in Pyramid Lake from February through November 1977.

tributed in vertical strata exhibiting temperatures less than 21.0 C. The preferred temperature and associated depth distribution is species-specific; e.g., kokanee (*Oncorhynchus nerka*) were primarily found at temperatures of 10.5–15.5 C (Horak and Tanner 1964). The vertical distribution of cutthroat trout in a large Montana reservoir indicated that their preferred temperature was in the 15–17 C range (Steven L. McMullin, letter dated 30 September 1977). This observation is in accord with Dwyer and Kramer's (1975) findings that the scope for activity of cutthroat trout was maximum at 15 C.

The fact that I observed maximum cutthroat trout densities in vertical strata exhibiting relatively low temperature ranges may be attributed to a lower temperature preference of the Lahontan cutthroat subspecies, or synergistic interaction between temperature and the high alkalinity levels of Pyramid Lake. Preliminary evidence indicates that as alkalinity concentration increases from the level of fresh water (<100 mg/l) to Pyramid Lake water (>1400 mg/l), the lethal temperature range is considerably lowered (Vigg and Koch 1978).

The periods of maximum surface orientation of the cutthroat trout population corresponded to the spawning run at the Marble Bluff fishway (April–May) and the maximum activity of the trout in the lake (December) (Vigg 1978b). The temperature regime of the surface waters functions as a gateway, allowing access from the hypolimnion of the lake through the shoals and into the Truckee River. This "gateway" is open during spring and again in early winter; interacting with river flows and temperatures, the lake's temperature mechanism thus delimits the potential spawning periods of the cutthroat trout population. Snyder (1917) documented that historical spawning runs of Pyramid Lake Lahontan cutthroat trout originally occurred both in early winter and spring.

The response of tui chubs to the temperature regime was nearly opposite that of cutthroat trout. The proportion of the tui chub catch taken in the surface waters was directly related to temperature from February through June; as temperature increased

from 6.6 to 16.3 C, the proportion of the catch/effort per unit of net area taken on the surface increased from less than 10 percent to over 75 percent. The mean proportion on the surface during July and August was about 51 percent, at surface temperatures of about 22 C. Temperatures declined from 21.2 C in September to 14.5 C in November; during this period the percent of tui chubs taken in the surface samples had decreased to about 20 percent. This movement of tui chubs from surface to benthic areas during fall is consistent with previously documented onshore-offshore benthic distribution patterns (Vigg 1978a). For example, during August 1977, 95 percent of the tui chub catch was taken in littoral (0–15 m) areas; by November, 64 percent was taken offshore at 46 m.

Similar *Gila* distribution patterns have been observed by other workers. Snyder (1917) reported an inshore movement of tui chub in Pyramid Lake in late May, associated with warm water temperatures and commencement of spawning. The Eagle Lake tui chub population also shifted in the spring from the deep waters inhabited during the winter into warming shallow waters (Kimsey 1954). The limnetic form of Lake Tahoe tui chub inhabits upper waters during the summer and disappears into deep water during the winter; the benthic form likewise inhabits deep water during the winter, but shallow littoral areas during the summer (Miller 1951). Gaufin (1964) observed that Utah chubs, *Gila atraria*, generally concentrated in the warmest areas of Fish Lake. Food consumption and assimilation, growth, and metabolic rates of Utah chub are directly related to temperature and are highest at 20 C (Cheng 1975). The Utah chub in Hebgen Lake, Montana, concentrated in shallow areas in the spring, were widely distributed in the summer and fall, and concentrated in deeper waters in winter (Graham 1961). In Flaming Gorge Reservoir, the Utah chub population moved into the littoral and eulittoral areas about a month prior to the commencement of spawning, which occurred mid-June through mid-July (Varley and Livesay 1976). This inshore movement corresponded to peak catches (activity) observed during July.

The offshore, limnetic tui chub population was surface oriented during the warm season. From June through October, about 92 percent of the limnetic tui chub catch was taken in the upper 23 m (Table 2).

Vertical limnetic distribution of tui chub is undoubtedly affected by temperature; however sampling was conducted during the warmest months of the year (June-October) when mean surface temperature ranged only 16.3–23.1 C. Therefore, all of the seasonal distribution patterns (e.g., downward winter shift) were not qualified by the vertical gill net sampling of the limnetic zone. Nonetheless, monthly changes in vertical distribution occurred within this upper temperature range. Maximum surface temperature (mean = 23.1 C) was associated with maximum occurrence (70.4 percent) of tui chub in the upper 7.5 m.

The temperature regimes in June (mean surface temperature was 16.3 and increas-

ing) and October (mean surface temperature was 16.5 and decreasing) were similar; likewise, the vertical distribution patterns of tui chubs were similar. During June and October, 94.8 and 90.8 percent, respectively, of the total catch was taken in the upper 15 m.

July and September also exhibited similar temperature regimes (mean surface temperature was 21.25 C) and similar (dispersed) tui chub distribution patterns. The 7.2–22.5 m depth interval was most abundantly represented, 72.6 percent of the total in July and 72.1 percent in September.

The limnetic tui chub population of Pyramid Lake is composed almost exclusively of the planktivorous (fine gill rakered) *pectinifer* form which feeds almost entirely on zooplankton (Langdon 1978). The vertical distribution of limnetic tui chubs was associated with that of the zooplankton they were selecting in their diet (Fig. 3). In June,

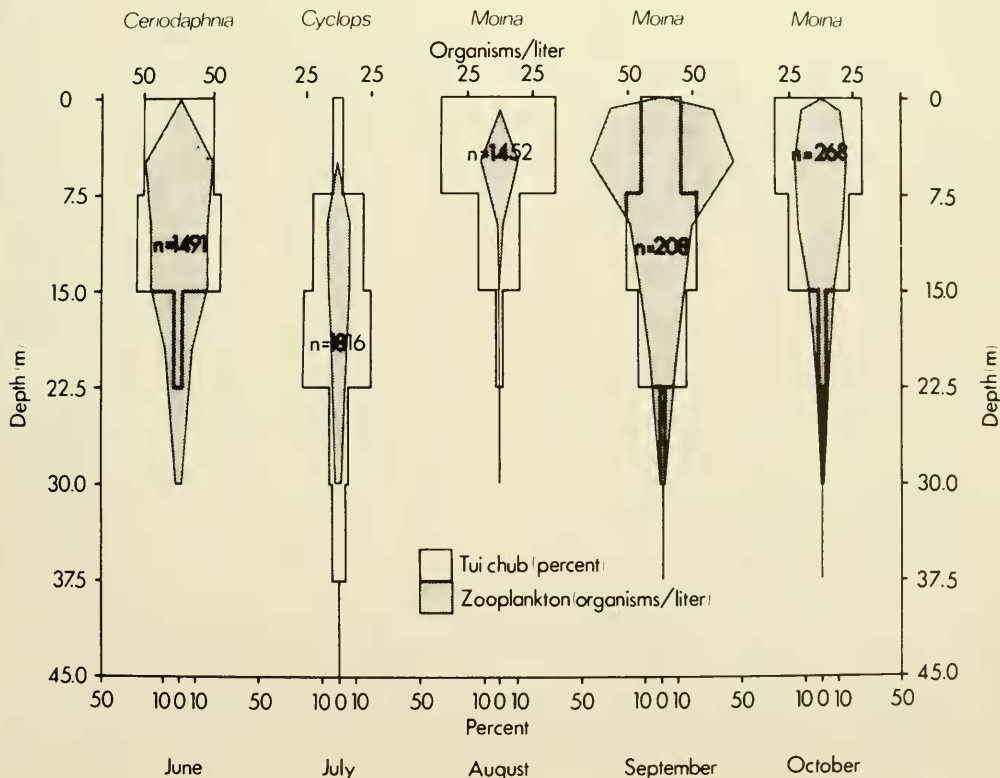


Fig. 3. Vertical limnetic distribution (percent by depth interval) of tui chub in Pyramid Lake, Nevada, from June through October 1977 in relation to the vertical distribution (density by depth interval) of the zooplankton taxon selected in the diet of tui chubs.

Ceriodaphnia quadrangula was very abundant in the upper 15 m, with decreasing density to 30 m; likewise, tui chubs were most abundantly represented in the upper 15 m, with an appreciable proportion to the 22.5 m depth. The selected zooplankton in July, *Cyclops vernalis*, was less abundant than *C. quadrangula* of the previous month; however, its absence in the surface waters and predominance in the 7.5–22.5 m depth interval mirrored the vertical distribution of the tui chub. The tremendous abundance of tui chubs in the upper 7.5 m in July may have kept the standing crop of its selected food item, *Moina hutchinsoni*, at low densities; and the vertical distributions of the fish and zooplankton were strikingly similar. During September the tui chub population was less dense (about 14 percent of the August level), and more evenly dispersed over the entire 0–22.5 m depth interval. Concurrently, *M. hutchinsoni* was very abundant in the same depth strata. *Monia hutchinsoni* populations were most dense in the surface waters; however, due to the relatively high proportion of zooplankton to fish, it is unlikely that zooplankton were restricting the distribution of tui chubs within the upper 22.5 m of the limnetic zone. Tui chub distribution shifted upwards into the 0–15 strata during October. *Monia hutchinsoni* was less abundant this month and showed a very similar distribution pattern to that of the tui chub.

The preliminary hydroacoustic survey conducted during April 1976 provided supplemental information on the vertical distribution of tui chubs. Apparently the upward vertical migration had already occurred by this early spring month; the limnetic tui chub population was concentrated in the 4–18 m strata, with appreciable densities extending to 48 m (Nunnallee et al. 1976). Concurrent total zooplankton densities exhibited a very similar vertical distribution pattern (Lider and Langdon 1978). Upward prevernal migration was substantiated by initial sightings of abundant tui chub schools on the surface in March—during weekly aerial observations, 1976–1978 (Joseph L. Kennedy, pers. comm.).

Thus, seasonal vertical migration of tui chubs are probably concurrent with inshore-

offshore distribution trends already documented. In summary, it is likely that temperature-related factors are directive influences on the fish and zooplankton which interact within their predator-prey relationships to form the observed limnetic distribution patterns.

Diel activity patterns and vertical distribution was determined during June and August 1977. Sampling was conducted over continuous 24-hour periods in the vicinity of Cormorant Rock (northwest Pyramid Lake). Surface and bottom gill net samples were taken at 4-hour intervals along the 23 m depth contour; i.e., a total of 24 net sets were made.

Tui chubs were predominantly taken on the surface, and cutthroat trout were predominantly taken on the bottom at 23 m. During both June (Fig. 4) and August (Fig. 5), however, fish catches exhibited consistent distribution changes with respect to time-of-day. Tui chubs were almost exclusively taken in the surface waters from 2000–0400 hours; the surface catch was negligible during the twilight and daylight hours. This could be attributed solely to net avoidance during daylight. For example, Lindenbergh (1976) attributed the absence of alewives (*Alosa pseudoharengus*) in the catch of vertical gill nets during the day to net avoidance, even though the net appeared invisible to divers in the water. However, my experience with surface gill net sampling indicates that if fish were present in appreciable numbers they would be captured. For example, I captured large numbers of suckers (*Catostomus*) and shiners (*Notemigonus*) in daytime, surface-set, white, multifilament gill nets in littoral areas of Ruth Reservoir.

I believe the observed patterns actually illustrate a movement of the tui chub population out of the surface into midwater. During both diel samples, the early morning movement of tui chubs out of surface waters corresponded to peak bottom catches at 0400–0800 hours. I think this represents an overcompensation in downward movement, which occurred when the bulk of the tui chub population moved to midwater. Similar over-compensatory vertical migrations of zooplankton after sunrise have been documented (Hutchinson 1967). The diel

vertical distribution of zooplankton closely corresponded to that of tui chubs. The prey species of zooplankton were most dense in surface waters from 2000-0400 hours and least dense at 1200; during midday, the

highest densities were observed at 5-10 m (Lider and Langdon 1978). Benthic densities of zooplankton were generally low during all time periods.

Very few cutthroat trout were captured

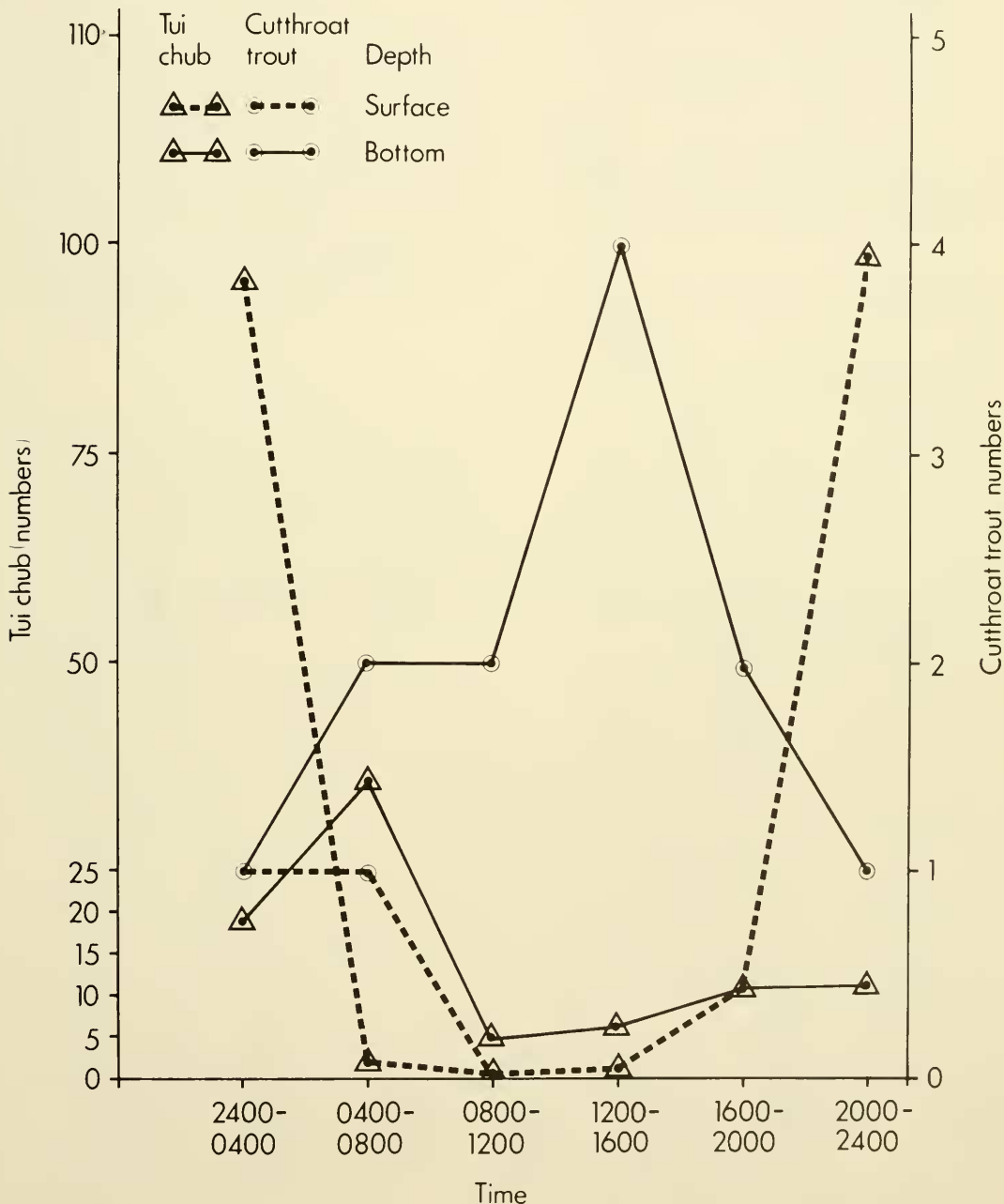


Fig. 4. Diel activity and vertical distribution patterns of tui chub and cutthroat trout at the 23 m depth in the vicinity of Cormorant Rock, Pyramid Lake, Nevada, during June 1977.

in surface nets. The morning hours (2400-1200) accounted for the entire surface trout catch. On the bottom, cutthroat trout catches were greatest during the daylight hours

(0400-2000). Because trout are sight feeders, it is logical that their activity would be greatest during this time period. Although no samples were taken midwater, I hypo-



Fig. 5. Diel activity and vertical distribution patterns of the tui chub and cutthroat trout at the 23 m depth in the vicinity of Cormorant Rock, Pyramid Lake, Nevada, during August 1977.

esize that cutthroat trout moved into the midwater zone during the daylight hours to feed on the tui chub population which was concurrently at maximum densities there.

ACKNOWLEDGMENTS

The Pyramid Lake Paiute Indian Tribe was instrumental in initiating the ecological research effort on Pyramid Lake. This research was funded by the Bureau of Indian Affairs, Contract H50C14209487. Mr. Floyd (Sam) Dunn and Mr. Dale Hebel carried out a great deal of the field work during this study. Mr. Edward Lider provided information on zooplankton distribution, and Mr. Richard Langdon provided information on tui chub diet.

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